

Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems

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(Received 4 December 2003; accepted 21 April 2004)

Abstract

Unsustainable hunting of wildlife or bushmeat for human consumption across the tropics threatens both wildlife populations and the livelihoods of people who depend on these resources. The probability that hunting can be sustainable depends in part on ecological conditions that affect the ‘supply’ of and ‘demand’ for wildlife resources. In this study, supply is estimated across a number of tropical ecosystem types by calculating the theoretical ‘maximum sustainable offtake’ in kg/km² for harvestable wildlife. Demand is estimated from observed harvests in kg/km². We examine how supply and demand vary across relatively undisturbed ecosystems, indexed by annual rainfall. Supply is potentially highest in dry forests and wetter savannah grasslands and decreases in moist forests and more xeric grasslands. Demand tends to exceed supply in moist forests and xeric grasslands. Analogous to this ecological variation along the rainfall gradient is the gradient created by the conversion of tropical forests by humans. We hypothesise that the wild meat supply is greater in secondary forests and forest–farm–fallow mosaics than in undisturbed forests and test this with available data. We conclude that the probability that hunting will be sustainable varies with ecosystem type and degree of human disturbance and should influence where land is zoned for protected areas and where for wildlife harvests.

INTRODUCTION

Hunting of wildlife for human consumption has been identified as both a conservation and a human livelihoods issue (Bennett *et al.*, 2002; Brown, 2003; Milner-Gulland *et al.*, 2003). Palaeontological and historical analyses show that hunting for human consumption is a conservation issue, because it can lead to population declines of target species (Bennett, 2000; Peres, 2000*a,b*; Steadman & Stokes, 2002), to local extirpations (Peres, 2000*b*) and even to global extinctions (e.g. Olson & James, 1982; Holdaway & Jacomb, 2000; Oates *et al.*, 2000). Hunting is especially problematic in the humid tropics, where the low biological production of large bodied animals frequently cannot meet the hunting pressure (Robinson & Bennett, 2000*b*). It is a human livelihoods issue because hunting results in the loss of wildlife resources for inhabitants of rain forests – some 60 million people in the forests of Latin America, South-east Asia and West Africa alone (Department for International Development, 2002). Many of these forest-dwelling people are divorced from national economies and have little alternative source of protein and income (Robinson & Bennett, 2002).

How to address the ‘bushmeat crisis’, as it is has been called in Africa, remains elusive. There are those that argue that the only way to save wildlife species is to stop hunting (Peterson, 2003) but, in many contexts,

prohibiting hunting for wild meat will be institutionally difficult, prohibitively expensive and can be challenged on ethical grounds (Adams & McShane 1992; Ostrom *et al.*, 1999). There are also those that argue that ‘the only hope for breaking the destructive patterns of resource use is to reduce rural poverty, and improve income levels, nutrition, health care and education’ (Brandon & Wells, 1992) – and to do so by promoting the trade in wildlife products, one of the few marketable commodities available to forest dwelling people (Biodiversity in Development Project, 2001; Davies, 2002; Department for International Development, 2002). This approach, however, can lead to rapid exploitation and deterioration of wildlife resources (Robinson & Redford, 2004).

The feasibility of different approaches depends in part on whether the organisational capacity exists to reduce or manage hunting. For instance, in Sarawak, the government has banned the commercial trade in wildlife in recent years, an action that has simultaneously benefitted wildlife populations and rural communities (Bennett & Tisen, 2001). In addition to this institutional context and management capacity, the feasibility of different approaches depends on the ecological factors that influence both the ‘supply’ of and ‘demand’ for wildlife resources.

This paper develops a broad, general assessment of ‘supply’ and ‘demand’ across tropical ecosystems. To assess supply we develop theoretical measures of the

maximum sustainable offtake and to assess demand we examine actual wildlife harvests. Neither supply nor demand is uniform across the tropics. Tropical landscapes are heterogeneous, with different wildlife communities and dynamics and different human pressures. Where observed demand is greater than potential supply, the harvest is clearly not sustainable. This analysis allows us to address the following question: under which ecological conditions and in which places is hunting for human consumption most likely to be sustainable? The answer should influence in what places hunting might be a management option and where encouraging or even allowing it will both extirpate wildlife populations and human aspirations.

Ecological conditions are affected by physical and climatic variables and by the degree of human disturbance. As an index of the first, we used average rainfall to order tropical sites along a gradient. To categorise the second, we somewhat arbitrarily distinguished three distinct conditions:

1. Relatively undisturbed ecosystems, where humans might or might not be actively involved in the harvest of natural resources and where humans modify and manage ecosystem processes only at local scales.
2. Human-influenced systems, where humans have converted and modified the ecosystem on a much wider scale – forests might have been cleared, agriculture might be a predominant activity, rangelands might support domestic animals – but wildlife still occurs in the more undisturbed habitats and can still be a resource for people.
3. Human-dominated systems, where humans have intensified agriculture and grazing systems, usually with extensive energy inputs (through fertilisers, herbicides and pesticides) and where most wildlife has been extirpated.

We analysed quantitatively how supply of and demand for wildlife resources vary across the rainfall gradient in relatively undisturbed ecosystems. We then discuss by analogy expected patterns of supply and demand in human-influenced systems. In human-dominated systems, wildlife as a resource has generally been extirpated and is not of interest in this discussion.

METHODS

To evaluate the ‘supply’ of wildlife resources across a range of relatively undisturbed ecosystems, we first examine the variation in standing biomass of large-bodied primates, ungulates and rodents (large-bodied is defined as species with average adult body mass equal to or greater than 1 kg), taxa that account for most of the wildlife biomass hunted by humans for food across the tropics (Robinson & Redford, 1991; Robinson & Bennett, 2000b). Sites for which this information was available were tabulated from the literature. Some of the estimates of biomass in more open habitats include the biomass of domestic animals (cattle of pastoralists or on open rangeland), following the argument that in the absence

of rangeland intensification, adding standing biomass of domestic animals gives a more accurate estimate than not of potential standing biomass of wild species (Stelfox *et al.*, 1986), although these estimates will tend to be high because domestic livestock biomass typically exceed those of wild ungulates (Eisenberg & Seidensticker, 1976; MacNab, 1991). We chose not to use the biomass estimates for African savannahs assembled by Coe, Cumming & Phillipson (1976) and Bell (1982) because of biases in the data set associated with aerial surveys of only ungulates (Caughley, Sinclair & Scott-Kinnis, 1976).

Any standing biomass generates an annual biomass production, which is defined as the addition to a population (through births and immigrations), whether these animals leave (through deaths and emigrations) or survive to the end of the specified time period (Banse & Mosher, 1980; Western, 1979; Robinson & Redford, 1991) and is at a maximum at the maximum species-specific intrinsic rate of natural increase (r_{\max}):

$$P_{\max(D)} = (D \times \lambda_{\max}) - D \\ = (\lambda_{\max} - 1)D$$

where D is the observed density of the species, λ_{\max} is the maximum finite rate of increase and is the exponential of the intrinsic rate of natural increase (e^r) (Robinson, 2000). Production can be converted into ‘Species Biomass Production’ by multiplying by the average body mass of the species, or into ‘Biomass Production’ for the entire harvestable community by the addition of all large-bodied primates, ungulates and rodents.

A certain percentage of this production can, theoretically, be harvested. That percentage, the maximum sustainable offtake in kg/km², is our measure of potential ‘supply’ of wildlife resources and can be estimated (Robinson, 2000) as:

$$(\lambda_{RR} - 1) \times 100$$

where

$$\lambda_{RR} = 1 + (\lambda_{\max} - 1)f_{RR}$$

where f_{RR} is a factor generally varying between 0.2 and 0.6, being lower with longer lived species. Estimates of the maximum sustainable offtake of some species have been developed empirically and theoretically (Slade, Gomulkiewicz & Alexander, 1998; Robinson, 2000). These estimates were used to approximate the collective offtake from the entire wildlife community. In using r_{\max} , these estimates assume the maximum possible sustainable offtakes. Where populations have already been severely reduced by long-term hunting, or where other factors are causing high mortality rates, sustainable offtakes will be lower than this (Sutherland, 2001).

To evaluate the ‘demand’ for wildlife resources, cases from the literature that recorded harvest in kg/km² were tabulated. As with the studies used to estimate supply, we restricted the analysis to harvests in relatively undisturbed ecosystems. These were not necessarily the same sites for which information on standing biomass was available.

Restricting the analysis to relatively undisturbed ecosystems, both supply and demand estimates were

Table 1. Biomass of large-bodied (> 1 kg) rodents, primates, ungulates and their totals at sites of different rainfalls

Site	Rainfall (mm)	Habitat	Rodents (kg/km ²)	Primates (kg/km ²)	Ungulates ^a (kg/km ²)	Total (kg/km ²)	Reference
Urucu, Brasil	3256	WF	70	391	341	891	Peres (1991)
Teiu, Brasil	2850	WF	?	?	?	1087	Ayres (1986)
BCI, Panama	2656	WF	300	482	542	2264	Eisenberg (1980)
Yavari Miri, Peru	2337	WF	63	441	319	823	Bodmer <i>et al.</i> (1994)
Ogooue-Maritime, Gabon	2200	WF	2	247	765	1050	Prins & Reitsma (1989)
Manu, Peru	2028	WF	129	655	403	1400	Janson & Emmons (1990)
N.W. Liberia	2000	WF		2076	933	3009	Barnes & Lahm (1997)
Parc des Volcans, Rwanda	1975	WF	?	?	?	3100	Plumptre & Harris (1995)
N.E. Gabon	1798	WF		692	1521	2213	Barnes & Lahm (1997)
Ituri, DRC	1700	WF		710	633	1344	Barnes & Lahm (1997)
Lopé, Gabon	1506	WF	5	319	2776	3101	White (1994)
Guatopo, Venezuela	1500	DF	280	139	270	946	Eisenberg (1980)
Piñero, Venezuela	1470	DF/GS	36	20	7952 ^b	8008	Polisar <i>et al.</i> (2003)
Masaguaral, Venezuela	1462	DF/GS	445	175	7875 ^b	8684	Eisenberg (1980)
El Frio, Venezuela	1399	GS	2564		18804 ^b	22405	Eisenberg (1980)
Nagarahole, India	1200	DF/GS	0	236	14860 ^b	15094	Karanth & Sunquist (1992)
Acurizal, Brasil	1120	DF/GS	50	20	3750 ^b	4130	Schaller (1983)
Manyara, Tanzania	1150	DF/GS			16933	16933	Runyoro <i>et al.</i> (1995)
Katavi, Tanzania	1100	DF/GS	?	?	?	23139	Caro <i>et al.</i> (1999)
Mara, Kenya	1000	GS			19200 ^b	19200	Stelfox <i>et al.</i> (1986)
Serengeti Unit, Tanzania	811	GS			4222	4222	Schaller (1972)
Serengeti, Tanzania	750	GS	11		11595	11606	Campbell & Hofer (1995) Hofer <i>et al.</i> (1996) Dublin (1995)
Ngorongoro, Tanzania	630	GS			10982 ^b	10982	Runyoro <i>et al.</i> (1995)
Siminjaro, Tanzania	600	GS			8209 ^b	8209	Kaharananga (1981)
Cerro Cortado, Bolivia	500	DF	520	10	343	873	A. Noss, pers. comm.
W. Ngamiland, Botswana	405	GS	?	?	?	203	Yellen & Lee (1998); Hitchcock (2000)

In all sites hunting is negligible, so mammals are assumed to be at or near carrying capacity (K). Blanks indicate that the biomass of this taxon at the site was negligible, question marks indicate that biomass was not specified.

Habitat: WF, evergreen wet and moist forest; DF, deciduous dry forest; GS, grassland savannah.

^aIncludes elephants and buffalo at African sites, elephant and gaur at Asian sites.

^bIncludes domestic livestock.

plotted against average rainfall at all sites, producing supply and demand curves across ecosystems. This allowed us to assess overall patterns of hunting sustainability across relatively undisturbed ecosystems. All variables were transformed to logarithms to the base 10.

RESULTS

Supply and demand in relatively undisturbed ecosystems

Variation in standing biomass

Ecosystem types are generally predictable from total rainfall, seasonality of rainfall, latitude, altitude and edaphic conditions (Holdridge, 1967). Following other authors (e.g. Coe *et al.*, 1976; Barnes & Lahm, 1997), we used annual rainfall as a simple index of ecosystem type to explore variation in standing biomass. Holdridge suggested that in the tropics, under conditions of low seasonality and at low altitudes, 'wet forests' can be supported in areas with rainfall above 4000 mm, 'moist forests' between 2000 and 4000 mm, and 'dry forests' between 1000 and 2000 mm. Between 100 mm and 1000 mm of rainfall, savannahs, scrub and even dry woodlands can

be supported, but little plant biomass can be supported under arid conditions of less than 100 mm of rainfall a year. Thus, plant biomass decreases steadily as rainfall declines.

Mammalian biomass does not decline across the rainfall gradient in the same way (Table 1). The three taxa most important for human consumption, large-bodied ungulates, primates and rodents, occur at different relative and absolute densities in different ecosystems, with ungulates predominating in open habitats and primates occurring most commonly in forested ones (Table 1). Eisenberg (1980) argued that mammalian biomass should increase with increased rainfall, but fall as forest canopy covers over habitat suitable for herbivorous ungulates. In wet and moist forest, much of the plant biomass is in the form of inedible tree trunks and most of the leaves are heavily defended by plant secondary compounds, such as lignins and toxins, so are inedible to most mammals (McKey *et al.*, 1981; Waterman *et al.*, 1988; Waterman and McKey, 1989). Moreover, a high proportion of the primary productivity is in the canopy and only available to relatively small mammals such as primates, sloths and rodents; food availability for large ungulates in tropical forests is low (e.g., Glanz, 1982; Hart 2000).

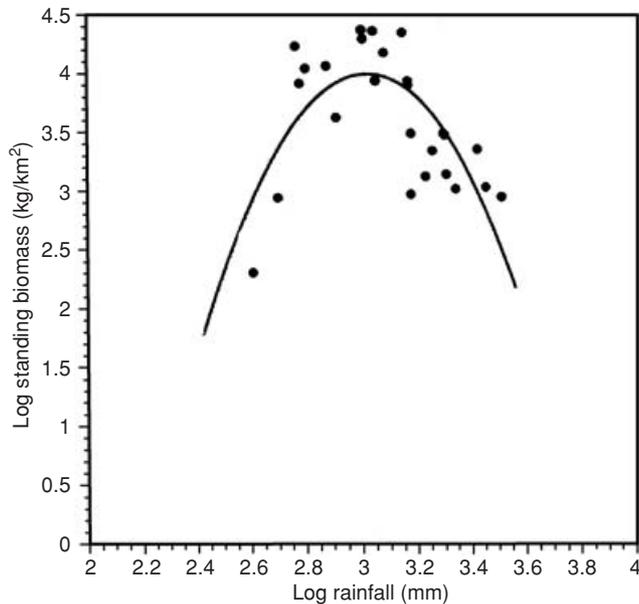


Fig. 1. Log_{10} biomass (kg/km^2) of ungulates, primates and rodents against Log_{10} annual rainfall at tropical sites. Data and their sources are listed in Table 1.

Figure 1 plots total mammal biomass against rainfall on log-log scales. Eisenberg's (1980) prediction that the relationship between biomass and rainfall can be described by a polynomial curve was strongly confirmed by Barnes & Lahm (1997). Biomass increases with rainfall but decreases with forest cover. Our analysis describes a very similar pattern to that of Barnes & Lahm (1997), although we include more tropical forest sites from Asia and Latin America and fewer savannah sites from Africa. The best polynomial model is:

$$y = -52.5 + 37.4 \text{Log}_{10}x - 6.2(\text{Log}_{10}x)^2$$

where $r^2 = 0.51$ and $n = 26$

Below 100 mm of rainfall, mammalian standing biomass is low, but grasslands with rainfall above 500 mm can commonly support mammalian biomasses of between 15 000 and 20 000 kg/km^2 . By contrast, the total mammalian biomass in tropical forests rarely exceeds 3000 kg/km^2 (Robinson & Bennett, 2000a).

Variation in the supply of wildlife resources

In addition to standing biomass, production is affected by the rate of natural increase (r). Species-specific maximum production rates can be calculated using intrinsic rates of natural increase (r_{max}) and totalled for the whole community of harvested species. For instance, Manu National Park in Peru has a standing mammalian biomass of about 1400 kg/km^2 (Janson & Emmons, 1990) and based on species composition, a maximum production of all the species of about 1076 kg/km^2 per year (from Robinson & Bennett, 2000a). The intrinsic rate of natural increase (r_{max}) of ungulates and rodents is much higher than that of primates at a specified body mass (Robinson &

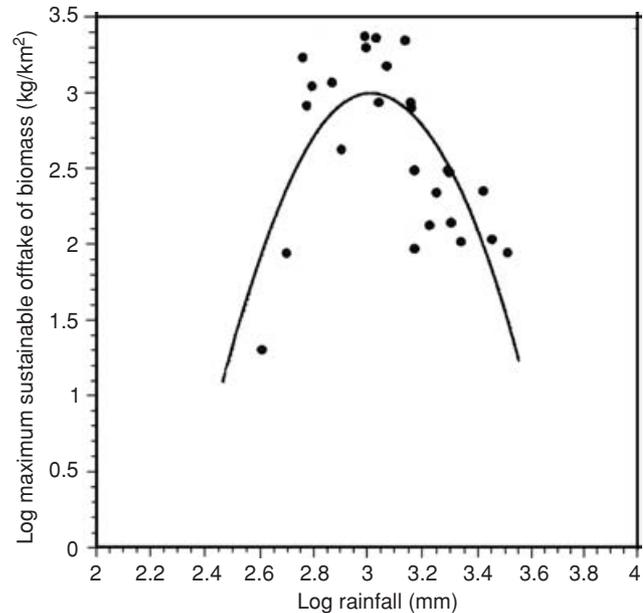


Fig. 2. Maximum sustainable offtake of Log_{10} biomass (kg/km^2) of ungulates, primates and rodents, a measure of potential 'supply', against Log_{10} annual rainfall at tropical sites. Maximum sustainable offtake was calculated as 10% of the standing biomass. The trend is probably more appropriate for moist and wet tropical forests and is conservative for dry tropical forests and savannahs.

Redford, 1986). Because ungulates and sometimes rodents dominate the biomass in more open habitats and they have higher rates of population increase than do primates, production per kg of standing biomass should be higher in savannahs than in tropical forests, where primates are more important.

Not all of this production can be harvested by human hunters, because of natural mortality in the population. The percentage that can be harvested without resulting in population decline (the maximum sustainable offtake rate) can be estimated for different species. In general, those percentages are lower for long-lived species. Annual offtake rates for some rodent species can exceed 50% of the standing biomass. Offtake rates for most ungulate species are generally lower, but frequently exceed 20%. Sustainable offtake rates for primates are low, usually under 5% of standing biomass (Robinson, 2000).

In drier, more open habitats (approx 500–1000 mm annual rainfall), the majority of the mammalian biomass comprises ungulates, so the average r_{max} of the mammals is greater and maybe as much as 20% of the standing biomass is potentially available for sustainable harvesting annually. In forested habitats (above 2000 mm annual rainfall), perhaps 10% is available for human harvests. For instance, Robinson & Bennett (2000) estimate that the maximum sustainable offtake for a wildlife community with a composition similar to Manu National Park would be about 152 kg/km^2 (about 11% of the standing biomass).

Figure 2 plots the theoretical pattern of maximum sustainable offtake along the rainfall gradient, estimated

Table 2. Biomass (kg/km²) of large-bodied (> 1 kg) primates, rodents and ungulates harvested at relatively undisturbed sites of different rainfalls

Site	Rainfall	Habitat	Biomass harvested (kg/km ²)	Human population density (#/km ²)	Reference
Bioko, Equitorial Guinea	5000	WF	55.9		Fa (2000)
Quehueiri-ono 1, Ecuador	2500	WF	146.9	0.91	Mena <i>et al.</i> (2000)
Quehueiri-ono 2, Ecuador	2500	WF	36.7	0.91	Mena <i>et al.</i> (2000)
Tahuayo, Peru	2337	WF	44.3		Bodmer <i>et al.</i> (1994)
Diamante, Peru	2100	WF	48.1	0.61	Alvard <i>et al.</i> (1997)
Yomiwato, Peru	2100	WF	20.6	0.27	Alvard <i>et al.</i> (1997)
Korup, Cameroon	2010	WF	217.0		Infield (1988)
Menembonembo, Sulawesi	1950	WF	701.0	300.0	Lee (2000)
Gunung Ambung, Sulawesi	1950	WF	462.0	300.0	Lee (2000)
Mbaracayu, Paraguay	1800	WF/DF	79.0	0.83	Hill & Padwe (2000)
Ibiato, Bolivia	1800	DF/GS	58.1	1.47	Townsend (2000)
Ituri, DRC	1750	WF	50.0	2.0	Wilkie & Finn (1990)
Ituri, DRC	1750	WF	60.3	2.0	Hart (2000)
Ituri CS, DRC	1750	WF	190.9	2.0	Hart (2000)
Ituri CR, DRC	1750	WF	209.7	2.0	Hart (2000)
Ituri SR, DRC	1750	WF	108.5	2.0	Hart (2000)
Dzanga Sangha, CAR	1400	WF/DF	125.0	0.98	Noss (2000)
Pandanguo, Kenya	1125	GS	2191.0		Harvey (1978)
Santa Anita, Bolivia	1100	DF	40.4	1.56	Guinart (1997)
Las Trancas, Bolivia	1100	DF	30.8	1.28	Guinart (1997)
Todos Santos, Bolivia	1100	DF	85.9	2.4	Guinart (1997)
Arabuko-Soko, Kenya	800	DF	348.9	35.8	FitzGibbon <i>et al.</i> (2000)
Serengeti	750	GS	774.0		Hofer <i>et al.</i> (1996)
Central Kalahari, Botswana	405	GS	11.0		Osaki (1984)
W. Ngamiland, Botswana	405	GS	1.3		Yellen & Lee (1976); Hitchcock (2000)

Habitat: WF, evergreen wet and moist forest; DF, deciduous dry forest; GS, grassland savannah.

at 10% of the standing biomass, which is probably appropriate for moist and wet forests but conservative for dry forests and savannahs. The best curve is:

$$y = -53.5 + 37.4 \text{Log}_{10}x - 6.2(\text{Log}_{10}x)^2,$$

$$r^2 = 0.51, n = 26$$

Variation in the demand for wildlife resources

Data on the biomass of animals harvested at specific sites across the rainfall gradient are uncommon, especially at low rainfall sites. The data that are available frequently do not specify the standing biomass of harvested animals, nor whether the harvest was sustaining or depleting species' populations. All of the data points in this analysis, however, were from relatively undisturbed ecosystems, not heavily influenced by humans (Table 2). We only included sites where hunting was not heavily capitalised or commercial.

Figure 3 plots actual recorded harvests of wildlife along the rainfall gradient. The best curve is:

$$y = -33.65 + 22.42 \text{Log}_{10}x - 3.5(\text{Log}_{10}x)^2$$

where $r^2 = 0.29, n = 24$.

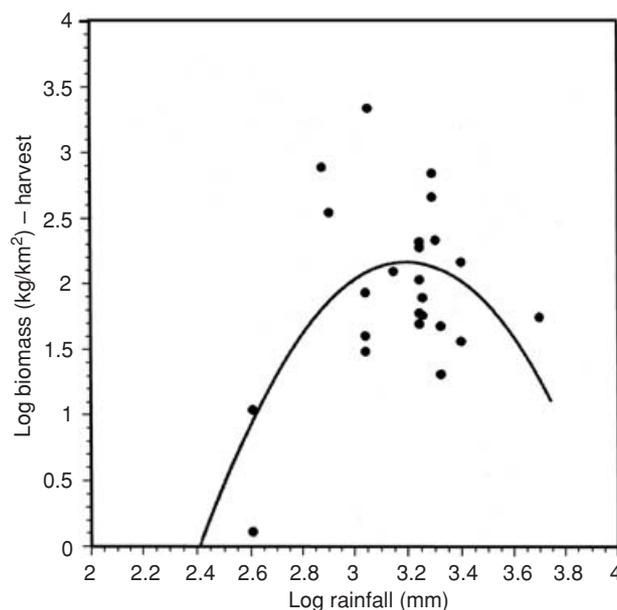


Fig. 3. Actual harvests of Log₁₀ biomass (kg/km²) of ungulates, primates and rodents against Log₁₀ annual rainfall at tropical sites.

FitzGibbon, Mogaka & Fanshawe (2000) suggested that subsistence harvest demand should covary with human population density. This sample confirms that expectation,

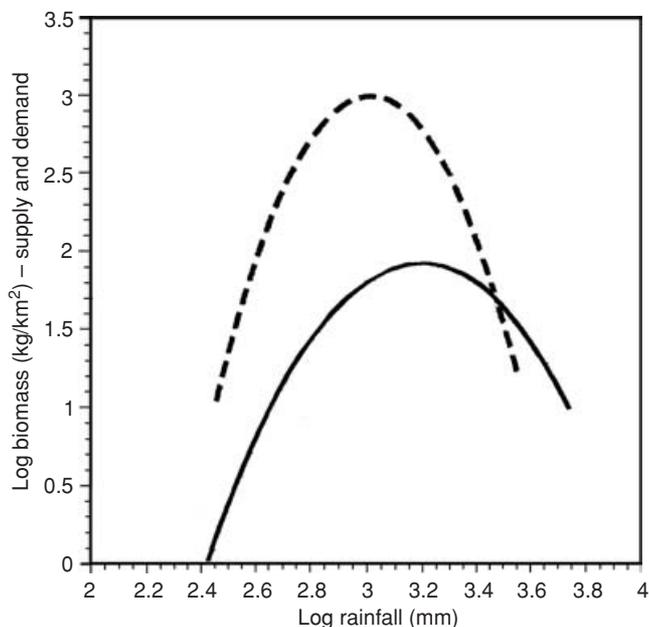


Fig. 4. Overlay of maximum sustainable offtake curve (= supply: broken line) and harvest curve (= demand: continuous line) plotted against annual rainfall at tropical sites.

even though sites were from across three continents and hunting technologies were quite different. Human density within or around sites where it could be estimated correlated with the total biomass of wildlife harvested from those sites (Spearman's $r_s = 0.61$, $n = 17$, $p < 0.01$).

Sustainability of hunting

At a given site, hunting will not be sustainable when harvest of wildlife resources consistently exceeds the maximum sustainable offtake. Figure 4 contrasts the generalised supply and demand curves for wildlife resources across the range of rainfall. At high rainfall sites, typically with wet forests, the overall trend using observed harvests is for harvest demand to be close to or to exceed supply, as assessed using the maximum sustainable offtake estimates. This accords with Bennett & Robinson's (2000) conclusion based on studies across tropical forests that 'hunting rates for many species generally are clearly not sustainable'. In contrast, at intermediate rainfall levels, between 500 and 1500 mm, characterised typically as dry forests and open savannahs, the high standing biomass allows a much higher maximum sustainable offtake and the pattern of observed demand indicates that harvests have a higher probability of being sustainable. At low rainfalls (below 500 mm/year), the pattern of harvest demand might again approach the maximum sustainable offtake.

In addition, harvest is more likely to be sustainable in dry forests and open savannahs because of the preponderance of ungulates and (especially in the neotropics) rodents. The intrinsic rate of natural increase (r_{max}) of ungulates and rodents in relation to their body

mass is much higher than that of primates (Robinson & Redford, 1986), allowing for a higher production, a higher maximum percentage sustainable offtake (Robinson, 2000) and a greater resilience to harvesting.

Supply and demand in human-influenced forested ecosystems

Variation in standing biomass

Analogous to the ecological continuum along the rainfall gradient is that created by human activities in tropical forests. Forests are commonly opened up by logging and other extractive activities and by conversion associated with swidden or shifting agriculture. Human activities thus create a gradient of ecological states that structurally mirror those determined by physical and climatic variables: logged forests, secondary forest mosaics, forest-farm-fallow mosaics and, eventually, field and pasture. Human activities lead to temporary elevated levels of nutrients for plant growth, higher light levels, more available browse and, thus, opportunities for herbivorous animals (Uhl *et al.*, 1990). A number of studies have examined wildlife biomass in logged forests and it is possible to separate out those cases where conversion is not associated with increases in hunting. Variation in the intensity of logging makes conclusions difficult, but the general trend is for the biomass of ungulates, after an initial decline, to increase in logged forests (for a summary, see Grieser Johns, 1997; Davies *et al.*, 2001). The response of primates is more species-specific.

By increasing the opportunities for herbivorous mammals, conversion of forest to more open habitats potentially might increase the standing biomass of large-bodied mammals. In practice however, this is rarely the case. Forest conversion is usually associated with the advent of people and there is a tight correlation between deforestation and human density (Green & Sussman, 1990; Meyerson 2000, 2003). While agricultural plots can provide additional resources for wildlife populations (Linares, 1976; Jorgenson, 2000), people depress standing wildlife biomass by introducing domestic livestock, which competes with wildlife species, and by hunting.

Hunting in secondary forest and forest-farm-fallow mosaics reduces standing wildlife biomass (Escamilla *et al.*, 2000; Lopes & Ferrari, 2000; Naughton-Treves *et al.*, 2003). Indications are that this is progressive, because areas with a long history of human habitation, hunting and agricultural activities, such as Quintana Roo, Mexico, only support a low biomass of wildlife (Jorgenson, 2000). Hunting also shifts the composition of the wildlife community, so that the biomass of large-bodied, slow reproducing species declines, while the biomass of more adaptable, rapidly-reproducing species, which are often, but not always, small-bodied, might increase (Wilkie & Finn, 1990; Lopes & Ferrari, 2000; Peres, 2000b; Naughton-Treves *et al.*, 2003). The consequence of this shift is that even though overall

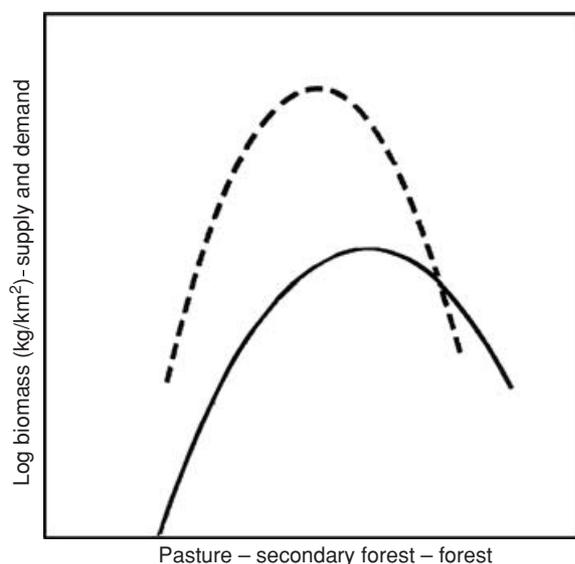


Fig. 5. Hypothesised supply (broken line) and demand (continuous line) curves in tropical forest areas that have been influenced by human activities, with relatively undisturbed forest being converted into secondary forests and pasture.

biomass might decline, biomass production might, under certain circumstances, increase.

Variation in the supply of wildlife resources

Figure 5 presents the hypothesis that the potential supply (= maximum sustainable offtake) of mammalian resources is higher in secondary forest/forest–farm–fallow than in relatively undisturbed forests. This is driven by a shift in the large-bodied mammal community from primates to ungulates and rodents with their higher r_{\max} . As conversion continues to pasture/field along the gradient, then supply is expected to decline as many forest-dwelling species are lost.

Data on biomass production from sites across the gradient of human disturbance are not available to test this hypothesis. However, some data are available from studies that have examined relative abundance of different wildlife species in different habitats – allowing an assessment of variation in biomass and how relative abundance of different species varies with body mass. Comparing four locations in dry tropical forest in Mexico that were characterised by different levels of forest conversion, Escamilla *et al.* (2000) report that wildlife abundance was higher in more disturbed areas and skewed towards small-bodied species. Comparing wildlife abundance in forests, farm–fallow and fields, Naughton-Treves *et al.* (2003) report significantly fewer records in fields than in either farm–fallow or forests, but as human disturbance increases, small-bodied, adaptable species predominate. Comparing different types of forest around two indigenous communities in Honduras, Demmer and Overman (2001) found that animal sightings and fresh tracks were more common in old-growth forests

than in human disturbed old-growth or in secondary forest and this was true for all species in the sample. Data are therefore equivocal, but do seem to suggest that in areas where hunting has not depleted wildlife populations, biomass in farm–fallow and secondary forest might be significant and skewed towards small-bodied and/or productive species, thus allowing higher biomass production than in less human-influenced systems.

Variation in the demand for wildlife resources

Figure 5 also presents the hypothesis that the demand (= observed harvest) for wildlife resources will first increase as forest is converted and then decrease as wildlife habitat is lost. The increase in harvest would be driven by an increase in human density and market integration. Local people hunt for sale as well as subsistence and outsiders gain greater access to the area, so overall hunting levels greatly increase (Auzel & Wilkie, 2000; Bennett & Gumal, 2001; Rumiz *et al.*, 2001; Wilkie *et al.*, 2001; Chin, 2002; Peres & Lake, 2003). Hunting pressure would be expected to increase as logging and colonisation open up the forest and as roads are built. Further along the disturbance spectrum, a decrease in harvest would occur as the process of forest conversion continues and natural habitat is lost, at which point other economic activities develop and people shift away from the use of wildlife resources (Ayres *et al.*, 1991). In areas where a high level of commercial harvest continues even after people's core livelihoods no longer depend on the wildlife resource, demand might still continue at a high level until the resource is largely depleted.

Available data generally support the hypothesis. Two studies have compared offtakes in forest and fallow/secondary forest. Wilkie (1989) reported that offtakes in secondary forests near villages were about 318 kg/km²/year, compared to 50 kg/km²/year in nearby climax forest (Wilkie, 1989). Furthermore, Demmer & Overman (2001) compared two communities of Tawahka Amerindians and found that extraction rates of most species were much higher in the community characterised by more extensive forest conversion. One study compared forest (not distinguishing primary and secondary) and gardens: Naughton-Treves *et al.* (2003) reported that mitayero hunters in Peru harvested roughly 15 times more meat by weight from forests than garden hunters (although the study did not calculate harvest rates/km²/year) and the average size of their prey was three times that of prey captured in fields. These studies thus generally support the hypothesis. However, in a study of four communities in Campeche, Mexico, Escamilla *et al.* (2000), found that the harvest rate of prey items was highest in the least disturbed area and there were more larger-bodied prey, while the harvest rate in the most disturbed area was greater than in the two intermediate areas.

The difficulty in testing the hypothesis is that studies to date have not controlled for other factors that influence demand. Even if there is a definable gradient of

disturbance, sites vary in: (1) degree of hunting protection or control (see Lopes & Ferrari, 2000); (2) the incentives for hunting, for example, the effects of wealth and market integration (Demmer & Overman, 2001); and (3) history of hunting, as evidenced by Quintana Roo, Mexico, which has a long history of hunting and where offtakes are only 3.3 kg/km²/year (Jorgenson, 2000). The large number of variables that affect hunting therefore require more careful analysis.

Sustainability of hunting

Forest dwelling people probably generally existed historically at densities of less than 0.1 person/km² (Denevan, 1992; Yalden, 1996). Forest dwelling people with small scale agriculture live at higher densities and densities of up to about 1.0 person/km² can continue to hunt most wildlife species sustainably (Robinson & Bennett 2000*b*). As human populations increase, even in forests that remain generally intact such as those in extractive reserves (Fearnside, 1992), the sustainability of hunting of many species is lost (Robinson & Bennett 2000*b*).

Figure 5 predicts that under certain circumstances, the probability of hunting being sustainable might be higher in secondary forests and secondary forest/pasture mosaics than in relatively undisturbed forests. Although demand might be higher because of higher human populations, these systems are likely to have a higher maximum sustainable offtake level.

The depletion of wildlife commonly reported for many secondary forest/pasture mosaics points out that this is not always the case. However, there are also clearly cases where hunting in these kinds of habitat appears to be generally sustainable. While offtake was low in the Maya communities of Quintana Roo, these people had been hunting in this area for over 4000 years and it is probable that hunting for at least many of the species was still sustainable (Jorgenson, 2000). A similar situation was reported by Cowlshaw, Mendelson & Rowcliffe (2004), who examined what they termed a 'mature' bushmeat market in Sekondi-Takoradi, Ghana. Wild meat was being harvested from the surrounding farmbrush matrix, a mosaic of plantations, remnant forests and fallow areas. Based on an analysis of price structure of wild and domestic meat, the researchers concluded that the harvest was sustainable. It is important to point out that in both of these cases, many of the large-bodied, slow-reproducing species that had been historically present in the area, were not harvested by hunters – presumably because populations had been depleted or driven to local extinction.

DISCUSSION

Millions of people in Asia, Africa and Latin America live at the margins of the cash economy and depend on the harvest of wildlife for subsistence and as a source of income. Those who see the 'resolution of the scourge of human poverty' as 'surely a supreme value' (Brown,

2003) suggest that the wild meat trade 'might be viewed in a highly positive light, as one of the great success stories of autonomous food production in the developing world, and a testimony to the resilience and self sufficiency of its populations'. Those who consider the stewardship of Earth's species as a supreme responsibility characterise the wild meat trade as 'a voracious appetite for almost anything that is large enough to be eaten, potent enough to be turned into medicine, and lucrative enough to be sold, is stripping wildlife from wild areas – leaving empty forest shells and an unnatural quiet' (Robinson & Bennett, in press).

These statements, while both have validity, run the risk of pitting advocates for the poor against advocates for the world's species. If turned into public policy, the first might argue for maintaining or expanding wildlife harvests to allow the capital accumulation essential for development – but this would ignore the fact that, in many areas, the present harvests are already depleting the very resources on which people depend. The second might argue for efforts to simply close down the trade, but would ignore the imperative that many people must harvest wildlife to survive. It is clear that arguing for a single blanket approach would be intellectually sterile and bad public policy.

This paper aims to distinguish the ecosystem conditions under which these different goals can be achieved, recognising that there is spatial heterogeneity in both the supply and demand for wildlife. Both poverty alleviation and conservation are important societal goals and the probability that they can be attained varies with place. Our analysis of the sustainability of hunting across ecosystems suggests that:

1. Dry forests and wetter savannah grasslands and mosaics of these, tend to have greater wildlife biomass and potential maximum sustainable offtakes than either (a) wet and moist forests or (b) drier grassland and arid zones. Notwithstanding the fact that actual harvests in dry forests/wetter savannahs can be greater than in either forests or arid zones, the differential between the general patterns of supply and demand increases the probability that hunting will be sustainable.
2. Secondary forests and forest fallow and mosaics of pasture and forests, which are created and influenced by human activities, might have greater wildlife biomass than undisturbed forest, a greater differential between supply and demand and a higher probability that hunting will be sustainable. This conclusion is less robust, because it is frequently the case that in these areas, characterised by the presence of large numbers of people, past harvests frequently have depleted wildlife populations.

There is broad recognition that wildlife harvests can be sustainable under conditions of very low demand, often associated with low human population density (e.g. Vickers, 1991; Bodmer *et al.*, 1994; Hill & Padwe, 2000). Here, we argue that sustainability might also be attained under conditions of high supply, even when demand is

significant. The suggestion that hunting can be sustainable under these conditions comes from studies in savannahs (Hofer *et al.*, 1996) and in secondary forests and forest fallow (Falconer, 1992; Jorgenson, 2000; Cowlshaw *et al.*, in press).

Our conclusion that savannahs might have a higher probability of sustaining a wildlife harvest does not indicate that these systems will ever contribute significantly to the provision of food security in rural areas. A succession of development schemes to harvest wildlife from African savannahs for the consumption of the rural poor ended in failure, constrained by the difficulty of harvesting on an economic scale and low sustainable offtake rates. MacNab (1991) concluded that:

‘... the hypothesis that game cropping would conserve wildlife and their habitats whilst providing a food source to the local people must be rejected... The history of game cropping schemes in the developing countries of Africa show that almost all were uneconomical or failed the test of sustainability.’

(John McNab is the collective pen name of four wildlife managers: A. R. E. Sinclair, D. Houston, G. Caughley and M. Norton-Griffiths). Neither does it indicate that these ecological systems will contribute significantly to the alleviation of poverty. To do so would require that rural people could accumulate capital from the sale of wild meat that would allow investment in alternative income-generating strategies. The numbers just are not there. Citing low maximum sustainable offtake rates for wildlife species, Brown (2003) argues that it is unlikely that ‘sufficient capital could be generated from the sector to sustain long-term economic change’ from the sale of wild meat.

Nevertheless, these ecological systems might very well have more potential to support harvests that act as ‘coping strategies and safety-net functions’ for rural people throughout the tropics (Brown, 2003). This conclusion is underscored in a number of studies that have examined wild meat hunting and consumption in rural communities, the inhabitants of which probably all fall under the definition of ‘extreme poverty’ with incomes of less than \$1 a day. Within these communities, it is the wealthiest that consume the most wild meat, but it is the poorest who hunt and/or sell the most wild meat (Eves & Ruggiero, 2000; Demmer & Overman, 2001; De Merode cited in Brown, 2003). Being able to harvest and sell wild meat is critical for these poorest of the poor.

While secondary forest/fallow systems are potentially important for human livelihoods, they are more incidental for conservation, since the large, slow reproducing species, those often of conservation concern, tend to be driven to local extinction. In contrast, relatively undisturbed forests are less productive for wildlife, for the majority of these species can only be harvested sustainably at extremely low rates. However, these systems are irreplaceable for the conservation of forest-dwelling species.

Land use planning must take into account the potentials of different ecosystems to accommodate different goals.

Relatively undisturbed forest is necessary for the conservation of many wildlife species while offering little potential for sustainable harvesting of wild species. Secondary forest/fallow might not have much value for conservation but might allow sustainable harvesting of wild meat for human consumption. However, it is not simply a question of appropriate zoning, since management decisions in one area can affect other areas. Allowing markets for animals harvested in secondary forest/fallow might undermine efforts to conserve wildlife in protected areas. Conversely, closing down commercial markets as an attempt to control hunting might adversely affect vulnerable rural people. Given this complexity, solutions to address the ‘bushmeat crisis’ will not be easy. But a first step is to recognise that the landscape is heterogeneous and that what might be possible as a management goal in one place might not be applicable in another. Only in this way will we be able to aspire to ‘sustainable landscapes’, which includes areas where we can conserve wildlife and areas where wildlife can be harvested, so that across the whole landscape, we can both have our wildlife and eat it too.

Acknowledgements

Discussions with Kate Abernathy, Guy Cowlshaw, Glyn Davies, Holly Dublin and Kent Redford prompted us to write this paper. The manuscript benefited from comments from Lisa Naughton-Treves, Guy Cowlshaw, Josh Ginsberg and an anonymous reviewer. Todd Olson and Andrea Heydlauff helped assemble the manuscript. To all, we give our thanks.

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